

Capsule Dehiscence in *Viola betonicifolia* Sm. (Violaceae)

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Summary

Little, J. & Leiper, G. (2012). Capsule dehiscence in *Viola betonicifolia* Sm. (Violaceae). *Austrobaileya* 8(4): 624–633. Seed dispersal syndromes in *Viola* are reviewed and the sequence of events culminating in the dispersal of seeds from capsules of *Viola betonicifolia* is documented. Seed parameters (length × width) and measurements of distances travelled after being ballistically ejected from a capsule valve were determined. Preliminary observations were recorded of the approximate length of time for a mature capsule to open and the approximate time for an open capsule to eject all seeds from its three valves.

Key Words: Violaceae, *Viola*, *Viola betonicifolia*, capsule dehiscence, diplochory, myrmecochory

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Introduction

The effective dispersal of seeds to sites where seedlings can successfully establish is critical to most vascular plants that reproduce sexually (Forster 2007). Understanding the methods by which seeds are dispersed provides valuable information about a species' potential for distribution and colonisation, and potential taxonomic relationships. Two distinct seed dispersal syndromes have been recognised in *Viola*: 1. **myrmecochory** (seed dispersal by ants following passive release from capsules) and 2. **diplochory** (explosive ejection of seeds followed by attraction and dispersal by ants) (Beattie & Lyons 1975). Characters attributable to the myrmecochory syndrome include a prostrate peduncle during dehiscence with the capsule on or near the ground; a calyx often swollen during fruiting; a capsule with walls not greatly thickened; seeds never under pressure during dehiscence; seeds with a large and conspicuous elaiosome; and seeds that are dispersed passively beneath the parent plant. Characters attributable to the **diplochory** syndrome include a tall peduncle that is erect during dehiscence and carries the capsule above the leaves; a calyx that does not enlarge during fruit development; a capsule

with walls thickened with sclereids that produce pressure on seeds; seeds with a small elaiosome; and seeds that are ballistically dispersed 1–5 m from the parent plant. A third type, called ballistic or **autochory** (explosive ejection of seeds away from the parent plant not related to ant dispersal) has been suggested for *Viola*, but was not detected as a distinct syndrome in the species studied by Beattie & Lyons (1975).

Perhaps the first documented observation of capsule dehiscence in *Viola* was that of Leavitt (1902) for *Viola rotundifolia* Michx., a perennial species from North America. Based on the distance that seedlings germinated in his garden from a single 'mother' plant, the species appeared able to ballistically eject its seeds 1.5–2.7 m (Leavitt 1902). Harrington (1903) stated, "after dehiscence [the capsule valves] fold lengthwise and eject the seeds with some force," and Bare (1979) said, "As each segment dries, it slowly folds together lengthwise, and the resultant pressure on the seeds throws them several feet through the air."

The method by which the capsules of diplochorous *Viola* species dehisce has been described variously as "sometimes dehiscing explosively" (Lawrence 1951),

“the matured capsule opens and ejects the seeds in a moment” (Ohkawara & Higashi 1994), “seeds are explosively ejected from the capsules” (Douglas & Ryan 1998), “opening \pm explosively on maturity” (Thiele & Prober 2003), and “at maturity the capsule springs open and the seeds are forcefully ejected” (Karlsson *et al.* 2012). These descriptions give the impression capsules ‘explode’ to release their seeds, in a manner similar to some genera in the *Euphorbieae* (Forster 2007). These descriptions obscure the actual mechanism by which capsules of many *Viola* species open and how the seeds are subsequently dispersed. Other workers describe how seeds are released from the capsule, e.g., “explosively ejected”, “ballistically dispersed”, or “ballistically ejected”, which more accurately describes how seeds are dispersed (Turnbull & Culver 1983; Bulow-Olsen 1984; Brooks & McGregor 1986; Douglas & Ryan 1998; Little & McKinney in prep). However, there appear to be no detailed studies for diplochorous species documenting the actual process by which *Viola* capsules open and how the seeds are dispersed.

This note focuses on *Viola betonicifolia* Sm. subsp. *betonicifolia*, a species native to Australia. This species possesses characters attributable to the diplochorous seed dispersal syndrome, i.e., a tall peduncle with the capsule above the leaves at the time of dehiscence, a calyx that does not enlarge when the capsule develops, seeds with a small elaiosome, and seeds that are ballistically ejected some distance from the parent plant.

During a visit by the first author to Queensland and New South Wales, Australia, from November 2011 through January 2012, an opportunity arose to observe mature capsules of *Viola betonicifolia* and *V. hederacea* Labill. splitting open and to observe how seeds were ejected from capsules of *V. betonicifolia*. The second author made numerous additional observations in 2012 of how capsules open in *V. betonicifolia* and documented distances that seeds were ejected.

Questions we attempted to answer in this study for *Viola betonicifolia* included:

- What is the sequence of events for the peduncle and capsule leading up to seed dispersal?
- Does the inverted peduncle of cleistogamous capsules remain pendant or become erect?
- How long does it take for a mature capsule to open?
- How long before seeds begin to disperse from an open capsule?
- Are seeds dispersed randomly from a valve, or is there a pattern (e.g., do seeds disperse first from the center, the proximal, or the distal ends of a valve)?
- What are minimum and maximum dispersal distances?

For comparison with other *Viola* species we documented the number of seeds produced by cleistogamous flowers (abbreviated CL, which are self-pollinated flowers, with minute or no petals); measurements of seed lengths; and morphological details of chasmogamous flowers (abbreviated CH, which are flowers with showy petals).

Materials and methods

There were two rounds of observations. The first author observed and photographed *Viola betonicifolia* plants near Mt Lindesay in south-eastern Queensland, in December 2011 and 20 January 2012 during visits with the second author. Initial observations of capsules opening and seeds being ballistically ejected were made by the first author on 22 January 2012 from a plant collected as a voucher specimen on 20 January 2012, but not yet pressed. In the field, the collected plant was placed in a cup of water. The plant had two capsules which for convenience are discussed herein as A and B. Capsule A was photographed at different intervals after it had opened until all seeds were ejected. The number of seeds in each valve was determined for Capsule A, as was the approximate length of time from when it began to open until all seeds were ejected. While attention was focused on Capsule A, Capsule B had opened and ejected an unknown number of seeds.

Observation of Capsule B began when it had a total of 10 seeds remaining among the three valves. For both capsules, the time of day and number of seeds remaining in each valve were recorded at periodic intervals and documented with photographs.

Although valuable data were obtained during this first period of observation by the first author, dispersal distances could only be roughly approximated due the fact that it was difficult to observe where the dehiscent seeds had landed. Dr Paul Forster encouraged the authors to gather better data on dispersal distances. The second author volunteered to continue a second round of observations and to measure dispersal distances and seed parameters. Eventually, container-grown plants were obtained and maintained outdoors by the second author in Beenleigh, Queensland. During this study, no CH flowers were present. Plants with CL capsules that appeared ready to open were brought indoors and dispersal distances were able to be measured under controlled circumstances. To determine dispersal distances, white flannelette sheets with roughened surfaces to minimize bounce of seeds were placed around the containers and the distances where seeds landed were measured by two observers.

Photographs were taken of maturing capsules to document

- the movement of the peduncle;
- the position of capsules prior to splitting and opening;
- whether capsules open slowly or explosively;
- the number of seeds per capsule; and
- if seeds are randomly dispersed from a valve or if there is a pattern by which they are dispersed.

Seed measurements (length \times width) were made by the second author with a micrometer. Statistics were calculated with Microsoft® Excel.

Results

Viola betonicifolia subsp. *betonicifolia* is a perennial, acaulescent species native to the east coast of Australia from South Australia

and Tasmania to Queensland; it is also found in New Guinea and the Philippines. It occurs in a wide range of habitats from coastal dunes and sclerophyllous forest to alpine herbfields (Adams 1982). The species produces both CH and CL flowers. The species is available for horticulture commercially and is sold in Australia mainly through specialist native plant nurseries.

Floral Morphology

Fig. 1 is a typical CH flower of *Viola betonicifolia*. The lateral petals are bearded (Adams 1982; James 1990a,b). We found that CH flowers on some plants at Mt Lindesay also have hairs on the two upper petals (**Fig. 1**), which has not previously been reported. The CL flowers of *V. betonicifolia* have sepals but no petals (**Fig. 2**).



Fig. 1. Typical CH *Viola betonicifolia* flower; Mt Lindesay, Queensland. Photo: J. Little



Fig. 2. A CL flower developing from the base of the plant. Sepals are visible enclosing the ovary. Petals are absent. Photo: G. Leiper

Capsules

After the ovules are fertilized, the capsules of CL flowers begin maturing in an inverted position, typical of CL flowers of many *Viola* species. As the capsule matures the peduncle elongates, lifting the capsule to an elevated position above many of the leaves. It transitions from an inverted to an upright position in about 24 hours (**Fig. 3**). The capsule also becomes noticeably paler, possibly because the xylem ceases functioning. The capsule becomes dehydrated to facilitate splitting open and eventual seed dispersal. The number of fertile seeds can be counted when the capsule is upright. In about another 24 hours, the capsule begins to split open (**Fig. 4**), the three valves begin to spread back and become completely separated (**Fig. 5**). Eventually the valves become more or less parallel to the ground (**Fig. 6**). Occasionally, a few seeds are ejected before the capsule is fully open.



Fig. 3. Capsule from CL flower on peduncle transitioning from inverted to upright position. Photo: G. Leiper

As the capsule valves begin to dry, the edges move toward each other. The pressure of the constricting valves squeezes the seeds which eventually causes them to be ballistically ejected. We observed that seeds at the distal end of valves were ejected first (**Fig. 6**) and those at the proximal end were ejected last (**Fig. 7**). However, for other capsules



Fig. 4. Capsule in fully upright position beginning to split open. Note shrivelled sepals. Photo: G. Leiper



Fig. 5. Capsule completely split open with valves beginning to spread apart. Each valve is ca. 13 mm long. Photo: J. Little



Fig. 6. Seeds in a valve about midway through dehiscence. Note the distal end of these valves contracted before the proximal end. Photo: J. Little

seeds at the proximal end were ejected first. Most capsules observed in this study ($n=7$) ejected all their seeds (**Fig. 8**).

Observations of Seed Dehiscence

Capsule A (recorded by first author): Capsule A was first observed open and in an upright position at 1121 with a total of 35 seeds (**Table 1**). The length of time it took to transition from an inverted to upright position was not observed nor was the time noted when the first seed was ejected. All seeds were ejected from the capsule in about 2.3 hr (138 minutes). Valve 1, which initially had two more seeds than the other valves, retained its seeds for a longer period of time. Valve 3 was the first to eject all its seeds.

Capsule B (recorded by first author): This capsule was first noticed when it was open and after it had ejected an unknown number of seeds. Observations of Capsule B began at 1603 when it had 10 seeds remaining (**Table 2**). Nine seeds were dispersed in the next 23 minutes. The time when the last seed was ejected from Valve 3 was not observed, but no seeds were present at 1715.



Fig. 7. One valve completely dehiscid; 2 valves with one seed remaining at proximal end of valve. Photo: J. Little



Fig. 8. Valves fully dehiscid and completely clapsed shut. Photo: J. Little

The second author timed a capsule that started opening at around 1400, was almost fully open at 1445, and was fully open at 1530. During the 45 minute interval between 1445 and 1530, some seeds were observed being ejected from the capsule. This capsule took about 1.5 hr to fully open and all seeds had been ejected by 1610. Thus, after it fully

Table 1. Seed dispersal times of *Viola betonicifolia* (Capsule A)

| Time | No. of Seeds in Valve | | | Total |
|------|-----------------------|---------|---------|-------|
| | Valve 1 | Valve 2 | Valve 3 | |
| 1121 | 13 | 11 | 11 | 35 |
| 1300 | 9 | 4 | 6 | 19 |
| 1303 | 8 | 4 | 6 | 18 |
| 1304 | 8 | 4 | 5 | 17 |
| 1311 | 5 | 4 | 0 | 9 |
| 1312 | 5 | 0 | 0 | 5 |
| 1338 | 2 | 0 | 0 | 2 |
| 1339 | 0 | 0 | 0 | 0 |

Table 2. Seed dispersal times of *Viola betonicifolia* (Capsule B)

| Time | No. of Seeds in Valve | | | Total |
|------|-----------------------|---------|---------|-------|
| | Valve 1 | Valve 2 | Valve 3 | |
| 1603 | 4 | 4 | 2 | 10 |
| 1604 | 4 | 3 | 1 | 8 |
| 1610 | 0 | 1 | 1 | 2 |
| 1626 | 0 | 0 | 1 | 1 |
| 1715 | 0 | 0 | 0 | 0 |

opened, it took 40 minutes until all seeds were ejected (some seeds dispersed before it was fully open).

Seeds

In the ovary, the ovoid-shaped seeds are attached to the placenta at the narrow end of the seed at the location of the elaiosome. Typical of many *Viola* species, the seeds are smooth and shiny when fully mature and fresh (**Fig. 9**). Mature seeds appear black or brown. Under magnification, they appear mottled black and brown (**Fig. 9**). The elaiosome is white or whitish when fresh (**Fig. 9**). The mean number of seeds per CL capsule was 19 ($n=7$ capsules, 133 seeds; range 8–35; SD 8.42; **Table 3**). The mean number of seeds per capsule is considered preliminary; additional counts need to be made utilizing a larger data set. Raw data for seed lengths and widths are available from the authors.

Mean seed length was 1.44 mm ($n=75$ seeds, five capsules); range 1.10–1.71 mm; SD 0.160. The length of five seeds was not determined because they were inadvertently



Fig. 9. *Viola betonicifolia* seeds emphasising elaiosomes. Lines are mm. Photo: J. Little

crushed when measured. The mean seed width was 1.11 mm ($n=74$ seeds, five capsules); range 0.98–1.30 mm; SD 0.075. The width of six seeds was not included because the colour of five was markedly paler than other seeds in the capsule and thus were assumed to not be fully mature and/or possibly not viable; another seed was inadvertently crushed when measured.

Dispersal Distances

The distances that seeds travelled after being ballistically ejected from capsule valves are summarized in **Table 4**. The mean distance for all seeds (n=85) was 148 cm; range 13–321 cm; SD 77.76.

The majority of seeds were dispersed a distance of 101 to 200 cm (**Fig. 10**). Two seeds exceeded 300 cm (306 and 321 cm).

Table 3. Numbers of seeds per capsule in *Viola betonicifolia*

| Capsule No. | Number of seeds |
|-------------|-----------------|
| 1 | 15 |
| 2 | 15 |
| 3 | 19 |
| 4 | 8 |
| 5 | 23 |
| 6 | 18 |
| 7 | 35 ^a |

^a Determined by first author; all others by second author.

Table 4. Seed dispersal distances in *Viola betonicifolia*

| Dispersal Date | Temp (°C) | Total number of seeds per capsule | Mean distance/ Range/ Standard Deviation (SD) | Distances (cm) |
|------------------|-----------|-----------------------------------|---|--|
| 19 February 2012 | n/a | 11 | 78.04 cm/ 17–154.5 cm; SD 41.36 | 17, 33.5, 37.5, 50, 72, 76.5, 95, 98.5, 106, 118, 154.5 |
| 22 February 2012 | 28.5 | 19 | 140 cm/ 13–256 cm; SD 66.36 | 13, 13.5, 56, 85, 90.5, 105, 132.5, 134.5, 139.5, 157, 159, 168, 174.5, 175, 175.5, 188.5, 210, 226.5, 256 |
| 1 March 2012 | 31.5 | 24 | 158.02 cm/ 27–253 cm; SD 67.85 | 27, 52.5, 55.5, 62, 79, 93.5, 104, 128, 133.5, 146.5, 161, 180, 188, 191.5, 198, 200.5, 204, 211.5, 213, 213, 224.5, 226, 247, 253 |
| 2 March 2012 | 31 | 15 | 181.16 cm/ 22.5–321 cm; SD 78.62 | 22.5, 83, 103, 141.5, 144, 150, 166.5, 177, 216, 217.5, 218, 226, 236.5, 295, 321 |
| 8 March 2012 | 28 | 16 | 161.06 cm/ 20–306 cm; SD 97.45 | 20, 33, 49.5, 76, 96.5, 106.5, 121.5, 141, 152.5, 177.5, 208.5, 215, 284, 294, 295.5, 306 |

Discussion

Cleistogamous flowers (CL)

We documented the presence of CL flowers in *Viola betonicifolia*. The presence or absence of CL flowers in this species is not mentioned in most Australian floras or guidebooks (Adams 1982; Stanley & Ross 1983; James 1990a,b; Robinson 1994; Entwisle 1996; Fairley & Moore 2000; Anon 2007; Duretto 2009; Elliot & Jones 2010). While not specifically mentioning cleistogamous flowers in *V. betonicifolia*, Williams (1979) referenced the presence of “self-pollinating flowers”. Of the 73 *Viola* species in North American, 60 are

known to produce CL flowers, nine species do not, and the condition in four species remains unknown (Little & McKinney in prep). The number of *Viola* species in the Australian flora that produce CL flowers has not been determined.

The fact that all CL capsules examined in this study contained mostly fertile seeds suggests that the pollination mechanism in CL flowers of *Viola betonicifolia* is highly efficient. Mayers & Lord (1983a,b) reported an interesting situation for *V. odorata* L. where the pollen grains in CL flowers germinate while still in the undehisced anther sacs; the

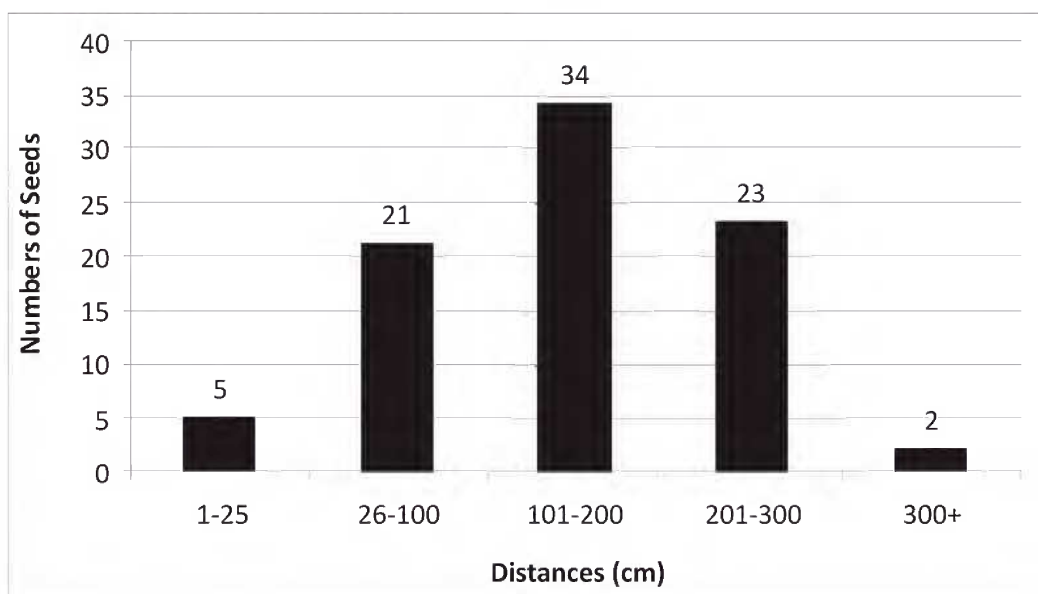


Fig. 10. Dispersal distance frequency histogram (n=84) for *Viola betonicifolia*

pollen tubes then penetrate the sac and grow out towards the nearby stigma. Karlsson *et al.* (2012) stated that preliminary observations in other *Viola* species suggest that pollen is simply released in close proximity to the stigma on the recurved style. The mechanism by which CL flowers of *V. betonicifolia* achieve self-pollination is unknown and needs study.

Capsules

Observations of mature capsules of *Viola betonicifolia* and other Australian species by the authors, and unpublished observations by the first author on several Californian species, show that the capsules of putatively diplochorous *Viola* species do not open ‘explosively,’ but instead open rather slowly. Based on this study and observations of other *Viola* species, the capsule itself does not ‘explode.’

Capsules of *Viola* species that disperse seeds ballistically are usually on erect peduncles, whereas capsules that passively release their seeds (e.g. *V. odorata*) usually point downward (Beattie & Lyons 1975). Capsules of *V. betonicifolia* are on erect peduncles prior to seed dispersal, typical

of diplochorous species that eject seeds ballistically. Upon drying, contraction of each of the three capsule valves squeezes the seeds, which are then ballistically ejected. We observed that *V. betonicifolia* seeds were sometimes ejected before the valves were completely open. This occurrence needs to be taken into account when determining the total number of seeds per valve and per capsule.

The morphology of mature capsules of CH and CL flowers are indistinguishable. Only CL capsules were available for this study. Dispersal in CH capsules has not been studied. However, based on observations of CH capsules of other *Viola* species in Australia and California, we suspect that CH capsules of *V. betonicifolia* dehiscence in a manner similar to CL capsules. Although empirical data are not available, it seems plausible that temperature, humidity, and soil moisture are important factors in the length of time it takes for a capsule to change from an inverted to an upright position, to split open, and to begin dehiscing seeds.

How long does it take a mature capsule to open? Based on one capsule that was timed, it took 1.5 hr to fully open. Although only one

capsule was timed, it was observed that all capsules opened slowly. None ‘exploded’ in a spontaneous release of seeds. After a capsule is fully open, how long before seeds begin to disperse? Data from two capsules showed that one took 2.3 hr while another took 40 minutes to disperse all their seeds. Are seeds randomly dispersed from a valve or is there a pattern? We observed that seeds were dispersed first from the centre and then randomly from either the proximal or distal ends of the valve. Beattie & Lyons (1975) observed that seeds of *Viola* species they studied were usually dispersed first from the centre of the valve.

Seeds and Dispersal Distances

The position of the individual valves relative to ground level prior to dehiscence affects the trajectory and dispersal distance for a given seed. The seed dispersal distances that we report are measures of the horizontal distance from the plant and may not reflect the actual distance travelled. For example, a seed could be ejected 200 cm vertically, but land only 20 cm from the plant. The dispersal distance in this case would be measured as 20 cm. We did in fact observe that some seeds were expelled vertically while others were expelled \pm horizontally. Further research is needed to determine if position in the valve correlates with the distance a seed is ejected, other factors being equal.

The mean dispersal distance for all *Viola betonicifolia* seeds was 149 cm ($n=84$), range 13–321 cm. The frequency histogram of dispersal distances approximates a bell curve (**Fig. 10**). Dispersal distances of seeds from *V. betonicifolia* CH flowers remain to be determined.

Beattie & Lyons (1975) reported distances of ballistically dispersed seeds for CH capsules of seven perennial *Viola* species native to eastern North America. They also reported data for CL capsules for three of the seven species they studied (*V. striata* Aiton, *V. blanda* Willd. and *V. papilionacea* = *V. sororia* Willd. var. *sororia*). Because dispersal distances of seeds from CH capsules were longer for each species compared to CL capsules, a reasonable comparison of Beattie

& Lyons’ (1975) data with *V. betonicifolia* was made by considering only the results from CL capsules: *V. striata*, mean dispersal distance was 110 cm ($n=50$), range 20–220 cm; *V. blanda*, mean dispersal distance was 80 cm ($n=18$), range 30–220 cm; and *V. papilionacea*, mean dispersal distance was 100 cm ($n=527$), range 2–210 cm. The mean dispersal distance of *V. betonicifolia* seeds from CL capsules (149 cm) exceeded the three species reported by Beattie & Lyons (1975) by 110, 80, and 100 cm. In addition, the maximum dispersal distance of *V. betonicifolia* (321 cm) exceeded the three species reported by Beattie & Lyons (1975) of 220, 220, and 210 cm.

Forster (2007) documented that ballistically ejected seeds of *Euphorbia obesa* Hook. (Euphorbiaceae) were viscid resulting in their sticking to soil, pebbles and vegetation. We found *Viola betonicifolia* seeds were buoyant in water, but not viscid and thus do not stick to surfaces. In coastal areas of Queensland, *V. betonicifolia* grows with *Melaleuca quinquenervia* (Cav.) S.T.Blake in swampy areas that become seasonally or periodically inundated from rainwater. In addition to ants, seed dispersal may be facilitated by being buoyant and transported in water during storm events. The potential that dispersal of *Viola* seeds can be facilitated by water has not been investigated. Anecdotal observations of *V. betonicifolia* plants growing in ‘lines’ in coastal wetlands in Queensland where water has obviously carried them and receded (pers. comm., F. Jordan), suggests that water dispersal may be an important, heretofore overlooked mechanism for dispersal of this species in Australia.

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